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The Love and Life of Fiddler Crabs

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(*With six plates*)

Back in 1953 I met the first fiddlers of my life on a muddy stretch of beach some 15 miles from Bombay. These swift-footed and keen-sighted crabs (genus *Uca*) inhabit the mud banks and sand shores, sometimes by the thousand—as seen from a distance. But as soon as I tried to approach their living quarters the flat seemed completely deserted. Walking across a fiddlers' mud flat is like wading through some miraculous lake with the waves receding before one's feet: in front, the waves of hundreds of fiddlers vanish with the crabs dashing underground into their burrows, only to emerge again in the wake of the person causing the general alarm. Thus, in spite of patience and tele-lenses I did not get any satisfactory shots of live fiddlers that year (R. Altevogt 1955 a, b) and was comforted only by the thought that even in the 'professional' literature there were hardly any.

But in 1955 I was back in India. This time it was only fiddlers, and my wife was with me to assist in observation and perseverance. We were settled to spend a full Indian summer on nothing but crabs on the beach. Much was to be done as there were quite a number of blank spots on the behaviour chart of tropical crabs in general and of fiddlers in particular. There were open questions with regard to the feeding technique of these mud-eaters; the 'meaning' and function of the waving movements of the crabs' big claws was still an argument among some zoologists; and nobody had so far seen any copulation in the Indian species, the total number of fiddler copulations seen in

the field amounting to a meagre five witnessed some years ago in the Americas by Miss J. Crane (1941-1944).

There we sat on the sunbaked beach and waited for the turn of the tide and for the fiddlers to come out of their holes in which, guided by some miraculous rhythm, they know how to spend the high water period. And no sooner had the water left the mud flat than the first fiddler peeped out of his, or rather her, hole, for she was a female. Somewhat dazed by the glaring brightness after the dark six hours underground, she made an easy victim for a forced portrait on my wife's thumb. Watching her running along in the field she seemed a terrifyingly small object for the camera's eye though she was of quite an average fiddler's size. The largest Indian species (*Uca marionis*) is at best about 32 mm. broad at the 'shoulders' (i.e. front of carapace) and, because of their extreme shyness, photographing fiddlers in the field is about as difficult as camera-stalking the domestic fly in the laboratory (though the latter activity definitely affords less perspiration). Gradually the flat became covered with fiddlers, all feeding eagerly. The females with their small claws of equal size used them alternately in picking up 'handfuls' of mud while the males could only eat with one hand, one of their claws being grossly enlarged to serve less 'primitive' functions than eating. Weeks later we had found out about the mechanism used in separating the edible contents from the inedible material of the soil. Highly specialized mouth parts with hundreds of 'spoons' on tiny hairs strain out the particulate matter from the mud in a process comparable to the flotation procedure of the gold washer with bowl and sieve. The coarse particles of the soil are rejected from the mouthparts and deposited in the form of pellets besides the advancing crab. Typical patterns are thus formed on the ground which have also been found in fossil deposits and were mistaken for extinct starfishes and crinoids.

With the feeding activity ceasing, the fiddlers entered the second phase of their daily routine, that of waving, fighting and copulating. 'Waving' denotes a typical movement which gave the fiddlers their popular name and which has been referred to as 'beckoning'. The type of waving differs with the species. In the Indian *Uca marionis* it is a relatively simple affair: the animal rises on tiptoes, and at the same time the major cheliped moves upwards and outwards. According to motion picture analysis this takes from $\frac{3}{4}$ up to several seconds. Then follows a very precise-looking and constant downward and inward movement of the claw during which the body is lowered again to its normal position touching the ground. After at least $\frac{3}{4}$ of a second the next waving movement is commenced, and

Fig. 1. Typical habitat of fiddler crabs.
Sympatric population of *Uca annulipes* and *Uca triangularis*. (After R. Altevogt 1957b)

Fig. 2. Fiddlers migrating to new habitats (see text)

Photos : R. Altevogt

Fig. 3. Female (left) and male *Uca marionis* feeding mud. Scale 1 cm.

Fig. 4. Traces of mud-feeding fiddlers : rejected mud balls in linear patterns radiating from crab's hole. Scale 10 cm.

Photos : R. Altevogt

so the crab goes on and on, often for hours. In another smaller Indian species, *Uca annulipes*, waving is quite different and shows a wide outward flexion of the cheliped to an extremely lateral position and then a rapid inward and downward movement. Travellers in the tropics have time and again been fascinated by the attractive spectacle offered by a densely crowded population of waving fiddlers, and there has been much arguing about the meaning and function of this remarkable feature.

We thought of all this while sharp shells gradually made their way through the mud to our naked feet, and the field glasses before our eyes became wet with perspiration. Six hours of low tide on a steamingly hot muddy or sandy beach is quite a long time when you have to sit absolutely motionless on some barnacle-fringed stone with your feet in an oozy mud of some 105 degrees F. and yet, what an exciting experience was provided by each ebb tide session out on the beach through all the months. The slightest motion on the part of the observer sends the fiddlers scuttling down their holes. Thus, it was exasperating, when Leica and movie tele-lenses had been carefully focussed on a spot where we confidently expected a fiddler's copulation or some ardent fight between two rival males to take place or a nuptial couple to indulge in love affairs, to find this happening in an adjacent spot just out of the camera's range and focus!

Finally, however, we learned how to 'handle' the fiddlers, and were able to make a full movie (R. Altevogt 1957 a) on their life and love. Almost every scene had to be taken with reasonable teles, and the quick movements of the tiny animals rapidly changing their distance from the cameras made sharpness of definition and focal depth quite a problem.

I would not say that in the long run the fiddlers of Bombay, Madras, and Rameshwaram fed right from our hands, but feed them with sweets we did, offering paper rolls soaked with sugar solution. Remarkably enough the little gourmets very readily found out the genuine sugar 'candies' from the array of paper rolls presented them soaked with solutions ranging from bitter quinine and salts to artifical sweetners like saccharine and dulcine. The fiddlers' ability to distinguish genuine sugars from artificial sweet substances in choice tests is shared, for instance, by the honey-bee (but not by the domestic chicken). If offered food which was different from the usual mud diet, our fiddlers would always prefer the former. This fact suggests that it may be out of selectional and ecological competition and necessity that fiddlers were forced to take to their

difficult and time-consuming technique of mud-feeding a long time ago in the course of evolution.

The love affairs of fiddlers are highly intricate. In order to shadow the individuals and to trace their ways through the crowds of fellow fiddlers we painted several dozens of them with bright colours using my wife's nail polish as the base to make the colours last through the high and low tides for several days. We thus found out that individual crabs left their living place, supposed to be their 'territory', all of a sudden and without any apparent reason, moving away as far as 66 m. from their first hole within the period of four hours. There were many others travelling 30-40 m. within the same period. Sometimes groups of 20-25 fiddlers, male and female, would gather, form a 'goose line', and leave their native quarter to migrate to a new habitat which did not differ a bit with regard to its ecological data—pH, moisture, temperature, salinity, and so forth. Such a striking behaviour sometimes reminded us of the routine migrations of 'army crabs' on the shores of south-east Asia and Australia. Apparently, however, one must group such spontaneous mass migrations under the heading of 'sport' as there is no apparent reason for the animals to indulge in this kind of 'wanderlust'. Sporting in fiddlers is also seen when a couple, or two or three Ucas run closely together and seem to really enjoy it. As such sprinting couples are sometimes males only, sometimes females only, and sometimes mixed, the activity seems to have no sexual significance, and one cannot but call it 'sport'. There is another kind of sport in some American fiddler species: sometimes funnels or igloo-like superstructures are erected over the entrance of the holes (fig. 7, showing such structures in the closely related Indian *Dotilla blanfordi*, another crab of the fiddler family), and repeatedly fiddlers have been seen to deliberately tear down the neighbour's igloo. Others seal the entrance of the neighbour's hole by plugging it with mud balls. Thus, quite a number of almost human 'nasty' traits of behaviour can be seen on a fiddlers' beach.

Almost human, too, are the females' reactions to the males' often frantic waving efforts. In *Uca marionis*, the largest Indian species, this is not nearly so pronounced as in the smaller *Uca annulipes* or *Uca triangularis*. In the former, the males, becoming pale white with excitement, chase the females often over a considerable distance always waving their claw until they finally get hold of the female and mount her for copulation. Surprisingly enough, this had not been observed so far by former authors reporting on *Uca marionis*, and this lack of information was apparently one of the reasons for the assumption that waving in fiddlers was a means of demarcating

Fig. 5. Male *Uca annulipes* feeding sugar-soaked paper rolls in choice test. Scale 10 cm.

Fig. 6. Male fiddler crab (*Uca marionis*). Note big waving and small feeding claw. Stalked eyes can be folded down sideways. Scale 1 cm.

Photos : R. Altevogt